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Modes of Feeding in Aggregations of Barnacles and the Shape of Aggregations

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Abstract. The interactions between the form of a barnacle aggregation, its flow environment, and the feeding behavior of each individual was determined in unidirectional flows; both models of barnacle aggregations and live barnacles were used. Hill-shaped aggregations of model barnacles captured significantly more particles than flat aggregations. In general, rows upstream of, and at the peak of, all hill-shaped profiles captured significantly more particles than downstream rows. Living barnacles located at, or upstream of, the peak of natural clusters captured significantly more food particles than did barnacles located downstream. Living barnacles located at, or upstream of, the highest point in a natural cluster fed passively, whereas barnacles downstream of the peak actively swept their cirral net against the flow. Flow was laminar up to the highest point in natural clusters, whereas flow was both reduced and turbulent over the downstream portions. Individual barnacles within a cluster differ in their feeding rates and net energy gains, and therefore differ in their growth such that, in unidirectional flow, the peak of a cluster will shift upstream over time; in oscillating flows, the clusters will develop a symmetrical profile.

Introduction

Acorn barnacles are sessile suspension-feeding animals. The feeding apparatus, the cirral basket, is a sieve-like net (LaBarbera, 1984) that typically is oriented perpendicular to the direction of ambient flow (Crisp and Bourget, 1985). Barnacles can draw upon a repertoire of feeding behaviors (Hazlett, 1988; Okamura, 1990). Changes in food concentration or flow rates elicit different feeding behaviors, largely expressed in the motion of the cirral basket. A feeding barnacle may use any of three patterns of cirral basket movement: normal beat, fast beat, and extension (Crisp and Southward, 1961). When flow velocity exceeds some threshold value, barnacles shift from fast beat to extension feeding (Crisp and Southward, 1961; Trager *et al.*, 1990), switching from sweeping their cirral baskets through the water, to simply holding their baskets against the flow. These two feeding behaviors are also known as active and passive, respectively (Jørgensen, 1966).

Both Crisp and Southward (1961) and Trager *et al.* (1990) focused on single barnacles in analyzing this flow-induced behavioral change. However, barnacle cyprids are gregarious settlers (Knight-Jones, 1953; Wethey, 1984), a behavior that often leads to aggregations of individuals (clusters) that generally display a hill-shaped contour. A common form consists "of a cluster of individuals enormously elongated at the centre of the hummock, and decreasing symmetrically towards the periphery" (Barnes and Powell, 1950).

Several explanations have been put forward for the origin of hill-shaped aggregations. Barnes and Powell (1950) suggested that pressure from neighbors caused growth of the central barnacles to be constrained to the upward direction; "barnacle shell growth is very plastic and . . . whenever forces are applied to the shell, its shape becomes modified" (Bourget and Crisp, 1975; also see Crisp, 1960). Crisp and Bourget (1985) suggested that food capture played a pivotal role in the development of hill-shaped aggregations. If some barnacles in a heavily settled area captured more food than their neighbors, they could only display their good feeding fortune by upward growth. Because taller barnacles feed higher in the flow boundary layer, they sample a higher flow velocity than their shorter neighbors (Crisp and Bourget, 1985). Faster flow implies

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a larger volume of water sampled and hence more food particles encountered (Vogel, 1983); thus, if all else were equal, taller barnacles would tend to grow still more (Crisp and Bourget, 1985).

A combination of mechanisms probably underlies the origin of the hill-shaped form; constraints to lateral growth from the presence of neighbors, and differential food capture are probably both involved. To unravel the relative contributions of each of these factors is difficult because the interplay between them is probably highly species-dependent. We have chosen to focus on factors that underlie differential food capture among individual barnacles, on the assumption that differences in food capture will translate into differences in relative growth rate for all species of barnacles. Our primary emphasis was on the form of hill-shaped aggregations. Such aggregations can be viewed as either a transitory stage in the evolution of the shape of a cluster of barnacles, or as a stable assemblage which, once achieved, remains relatively constant despite the continued growth of its constituents and recruitment of new individuals. As we will show, these two perspectives are in fact compatible and converge to the same outcome.

To address this question, we have chosen to examine the distribution of food capture across hill-shaped arrays of "mock barnacles," using real clusters of barnacles to verify the relative particle capture rates observed with the models, and to determine the influence of different modes of feeding (active *vs.* passive). Our goal is to explore the correlation between local flow environment and location-dependent feeding rates in a barnacle cluster. This exploration is central to an understanding of food distribution patterns and the feeding behavior of individual barnacles in a cluster.

Materials and Methods

All statistical analyses were performed using StatView II (ver. 1.03; Abacus Concepts, Inc., Berkeley, California) run on a Macintosh SE/30 computer. All descriptive and test statistics of normalized capture values (NCV's; see below) were calculated after transforming the data as arcsin $\sqrt{\text{NCV}}$ (Sokal and Rohlf, 1981); the statistical values given below were back-transformed to normalized capture values. Unless otherwise specified, we have used a significance level of 5% in all statistical comparisons.

Mock barnacle arrays

Plastic cylinders of two heights (0.3 and 0.6 cm) were cut from commercial polybutylene tubing (0.97 cm diameter). The cylinders were filled with plastacene and positioned in direct contact with one another in 4 (wide) by 5 (long) arrays. Each row (line of cylinders perpendicular to the flow direction) consisted of cylinders or stacks of cylinders of the same height. Four mock barnacle clusters (Fig. 1) were constructed; the profiles produced were flat (all rows 0.6 cm tall), symmetrical (1.8 cm high peak in row 3), shifted upstream (peak in row 2), and shifted downstream (peak in row 4). We adopt the convention that row 1 is the extreme upstream row of a profile; row 5 is the extreme downstream row. To mimic barnacles engaged in passive suspension feeding, isosceles right triangles (base 1 cm) were cut from 250 μm (diagonal) mesh plankton netting and inserted into the plastacene on top of each cylinder so the plane of the triangle was perpendicular to the flow direction; the hypotenuse of the triangle was distal to the cylinder and horizontal.

The arrays were placed midway between the walls of a 15 $\times$ 15 cm cross section flow tank, designed following Vogel and LaBarbera (1978), that was filled with fresh water. The boundary layer at the leading edge of the array was approximately 0.5–0.8 cm thick, as estimated from the distortion of vertical dye fronts injected just upstream of the arrays. The tank was seeded with freshwater-soaked *Artemia salina* cysts stained with rhodamine dye. The number of *Artemia* cysts added was only roughly ($\pm$10%) standardized, but the nature of the comparisons made correct for variation in absolute particle concentration.

In the first series of measurements, each of the four mock barnacle arrays was placed singly in the tank and exposed to a unidirectional laminar flow of 4–5 cm/s for 10 min. The number of *Artemia* cysts captured by each mock barnacle was determined by removing the mesh net after each run and counting the stained cysts trapped on the net. Once attached to the net, the eggs were never observed to become detached either during removal from the tank or during counting; the cysts lodged in the mesh netting, and only after the mesh was dried could they be easily removed. Each profile was tested four times. Numbers of particles captured by each cylinder in a row were summed to give total row capture. Because the concentration of suspended particles varied between experimental runs, total capture by all rows in an array for each run was normalized to 100 particles and individual row totals appropriately scaled to yield normalized row capture values. Normalized row capture values are thus equivalent to percentage of total capture by the array.

In a second series of measurements, two arrays representing different profiles were tested simultaneously in the flow tank. These tests were conducted to allow comparison of absolute numbers of particles captured. The arrays were placed at equal distances from the flow collimator, symmetrically about the longitudinal midline of the tank, and exposed to a 4–5 cm/s flow for 10 min. Particle capture was quantified as described above. Symmetrical and flat profiles were simultaneously run in six trials, and the shifted downstream and flat profiles were simultaneously run in seven trials; the other potential combinations of profiles were not tested.

Living barnacles

Dome-shaped clusters of mixed *Balanus amphitrite* and *Balanus tintinabulum* were collected from rocks and buoys near Boca Raton, Florida on 7 August 1990. Flows in the environment where the barnacles were collected were primarily tidal; mainstream velocities in the vicinity of the clusters were approximately 5 cm/s as measured by timing movement of natural particles along a known distance. The clusters were shipped in Styrofoam containers to Chicago, where they were held in a 300-l aquarium filled with artificial seawater and fed every other day on newly hatched *Artemia* nauplii. Barnacles fed avidly on *Artemia* nauplii in the aquarium; molting was common, and the animals appeared to be healthy. Because *B. tintinabulum* was uncommon in these clusters, our observations were restricted to *B. amphitrite*.

Food capture was quantified for at least one barnacle in each of three positions (upstream, downstream, and peak) on the midlines of two clusters. For a third cluster, data were gathered only for barnacles in the peak and downstream positions. Clusters were placed individually in the flow tank (filled with artificial seawater) and subjected to a unidirectional flow of 4–5 cm/s carrying newly hatched *Artemia* nauplii. Individual barnacles were observed to switch from active beating to passive suspension feeding at local flow speeds of 2–3 cm/s. [Threshold velocity for switching from active to passive suspension feeding was determined by observing peak animals in natural clusters (which essentially see mainstream velocities; Fig. 2) while the mainstream flow speed in the tank was varied.] Feeding of individual barnacles was observed using a 3.5× binocular magnifier; data were restricted to continuous feeding bouts of at least 3-min duration. *Artemia* nauplii captured during a 3-min interval were recorded using a mechanical tally counter; a capture was scored when a brine shrimp was seen to contact the cirral basket of the barnacle and the cirral basket was subsequently retracted completely into the shell. Those barnacles for which food capture values were quantified were also videotaped while feeding, and the length of the extended cirral baskets were measured on a video monitor. Assuming that cirral basket growth was isometric, the relative areas of the cirral baskets of the barnacles observed was approximated by squaring their measured lengths.

The average frequency of cirral basket movement of individual barnacles was determined by measuring the duration of a sequence of either 10 or 20 retractions (for passive feeders) or beats (for active feeders). (Passively feeding barnacles frequently retract their cirral basket and then rapidly re-extend it. This behavior is distinct from the rhythmic beating of actively feeding barnacles.) A series of observations of 10 or 20 beats was recorded. Timing was begun either at the retraction (for passive feeders) or on the downstroke (for active feeders). Beat frequency of at least one barnacle in each of the three positions in a cluster (upstream, downstream, and peak) was determined. Beat frequency was measured only on animals whose particle capture rate had been determined; typically, we measured cirral basket beat frequency of a barnacle after we had measured particle capture in four feeding bouts of 3 min each.

To determine velocity distributions around the barnacle clusters, the midline of the cluster was illuminated from above with a 0.5 cm wide collimated light beam; the plane of the light beam was parallel to the flow direction. Photographs were taken using a 35 mm camera and macro lens; exposure durations were either 0.5 or 0.25 s. *Artemia* individuals illuminated by the light beam were imaged as streaks as they were carried with the flow; the streaks recorded on the negatives indicated both flow streamlines (by their path) and local velocities (by their length). The negatives were projected and the streaks superimposed by manual tracing. The length of the streaks were measured by digitizing the tracings on a Houston Instruments HiPad™ connected to an Apple IIc computer. These values, appropriately scaled to reflect true distances in the flow tank, were divided by the camera shutter speed to calculate the mean flow velocity along the streak. Accuracy of velocity measurements was approximately ±0.05 cm/s.

Results

Mock barnacle arrays

The mean normalized row capture values for the four profiles tested singly are given in Table I; the results are portrayed graphically in Figure 1. ANOVAs were performed on arcsine transformed normalized capture values for each profile (Table II), with the data grouped by row. As is apparent, patterns of particle capture across rows differ between the profiles. For the flat profile, the extreme upstream row (row 1) showed significantly higher nor-

Table I

Normalized row particle capture values for the four profiles of mock barnacle arrays (see Materials and Methods)

	Flat	Symmetrical	Shifted upstream	Shifted downstream
Row 1	95.0 (79–99)	24.1 (11–41)	35.8 (21–52)	29.8 (13–50)
Row 2	3.9 (0–16)	26.7 (21–33)	51.8 (27–76)	32.8 (19–49)
Row 3	0.2 (0–2.6)	41.9 (29–56)	1.3 (0–10)	4.9 (4.0–5.9)
Row 4	0.1 (0–1.9)	0.7 (0–5.8)	4.5 (0–21)	25.7 (13–41)
Row 5	0.1 (0–1.9)	2.3 (0–21)	2.3 (0–11)	3.7 (0–20)

Mean values were calculated from $\arcsin\sqrt{NCV}$ where NCV = the normalized capture values; the values given above were backtransformed to normalized capture values. Values given in parentheses are the 95% confidence intervals of the means calculated from the transformed values. In all cases, n = 4.

malized capture values than all rows downstream. The most downstream rows (rows 3–5) showed no significant differences in normalized capture values. The three hill-shaped profiles differed drastically from this pattern. For the symmetrical and shifted upstream profiles, the peak row and all rows upstream of peak showed significantly higher normalized capture values than did the rows downstream of the peak. The values for rows downstream of the peak were statistically indistinguishable. For the shifted downstream profile, the peak row and all rows upstream of peak (except row 3) showed significantly higher normalized capture values than did the row downstream of the peak.

Differences between normalized row capture values of the mock barnacle arrays were tested using two sample t-tests (Table III). Table III reveals significant differences in normalized particle capture between rows 1, 2, and 3 of the symmetrical and flat profiles; row 1 of the flat profile had a significantly higher normalized capture value than row 1 of the symmetrical profile, while rows 2 and 3 (the peak) of the symmetrical profile had significantly higher normalized capture values than the same rows of the flat profile. Downstream of row 3, there were no statistically significant differences between rows in the two profiles.

Comparing the shifted upstream and flat profiles, rows 1 and 2 showed significant differences in normalized par-

Table II

Analysis of variance of the differences in normalized particle capture between rows in the four profiles of mock barnacle arrays

	Flat				Symmetrical				Shifted upstream				Shifted downstream			
$F_{4,15}$	117.1				19.7				21.3				12.2			
Row	2	3	4	5	2	3	4	5	2	3	4	5	2	3	4	5
1	*	*	*	*	—	*	*	*	—	*	*	*	—	*	—	*
2		*	*	*		—	*	*		*	*	*		*	—	*
3			—	—			*	*			—	—			*	—
4				—				—				—				*

For each profile, the F value of the ANOVA is given; in all cases, the ANOVA's were highly significant ($P < 0.0001$). In the row matrix, significant differences are indicated by an asterisk (*); lack of statistical significance is indicated by a dash (—). Normalized particle capture values were arcsine transformed before analysis; differences between transformed normalized particle capture values were tested using the Fisher PLSD test.

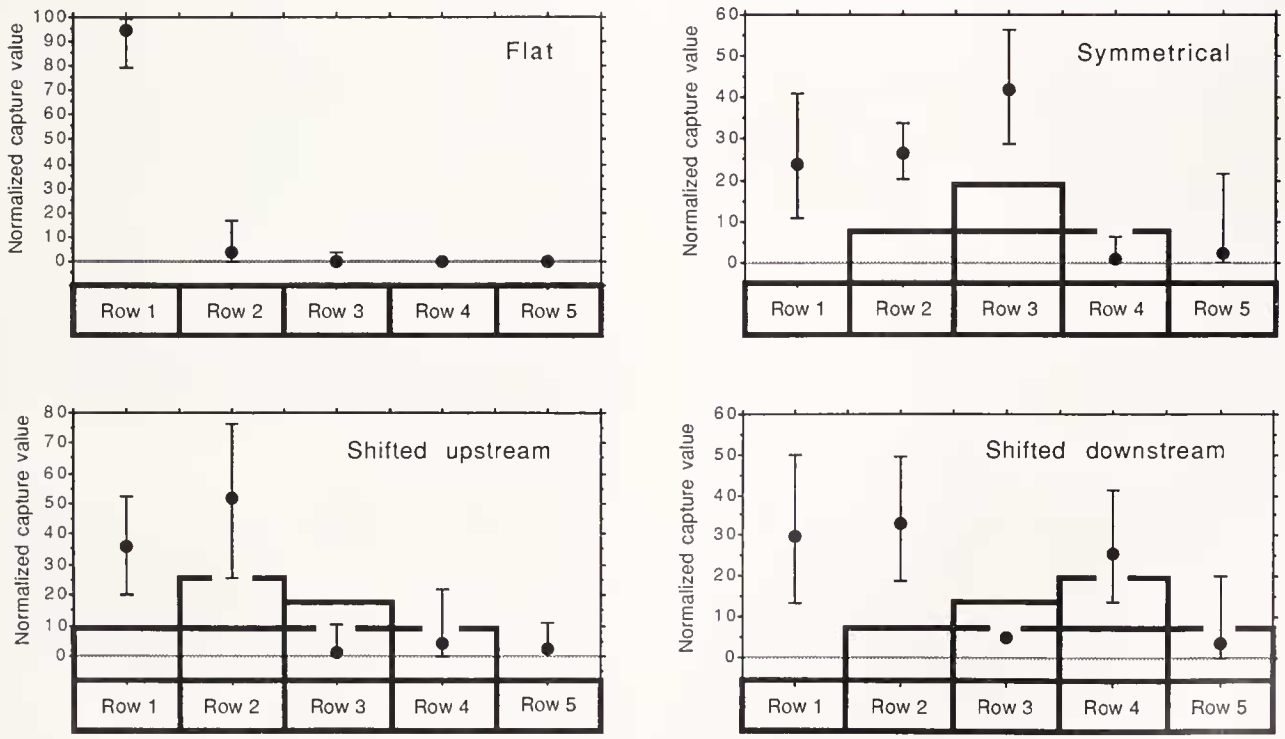


Figure 1. Mean normalized particle capture values (n = 4) for each row of various configurations of model barnacle arrays. Normalized particle capture = 100 ($C_r/\Sigma C_r$) where C_r = total number of particles captured per row. Ninety-five percent confidence intervals of the means are indicated by vertical lines; where no lines are visible, the confidence interval lies within the height of the point plotted. All arrays were tested individually in a unidirectional laminar flow of approximately 5 cm/s. The profile of each array is superimposed on the graphs; the upstream end (row 1) of each profile is on the left. Note that rows at or upstream of the peak of each array capture significantly more particles than rows downstream of the peak.

Table III

Two sample Student's unpaired t-tests of differences in arcsine-transformed normalized row capture values for the mock barnacle arrays tested singly in the flow tank

Row	Flat *vs.* Symm.	Flat *vs.* Shifted up	Flat *vs.* Shifted down	Symm. *vs.* Shifted up	Symm. *vs.* Shifted down	Shifted up *vs.* Shifted down
Row 1	8.53***	7.30***	7.59**	(−1.65)	(−0.76)	(0.73)
Row 2	−8.59***	−5.49**	−5.42**	(−3.07)	(−1.26)	(2.08)
Row 3	−9.20***	(−1.19)	−6.42**	8.37***	8.33***	(−1.44)
Row 4	(−1.09)	(−1.85)	−5.68**	(−1.50)	−5.39**	−3.61*
Row 5	(−1.11)	(−1.92)	(−1.47)	(0.43)	(−0.10)	(−0.65)

In all cases, n = 4 (df = 6 for each test). The values given are the t values. Values not significant at the $P = 0.05$ level are given in parentheses; asterisks indicate the level of significance (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). In all cases, a two-tailed test was used; probabilities were adjusted for multiple comparisons using the Bonferroni method.

ticle capture; row 1 of the flat profile had higher normalized particle capture values than row 1 of the shifted upstream profile, whereas row 2 (the peak row) of the shifted upstream profile had higher values. Downstream of row 2, there were no statistically significant differences in normalized particle capture.

Comparison of normalized row capture values of the shifted downstream and flat profiles revealed significant differences between the two profiles for rows 1–4; row 1 of the flat profile had significantly higher normalized capture values than row 1 of the shifted downstream profile, while rows 2–4 of the shifted downstream profile had significantly higher normalized capture than the same rows of the flat profile. (Row 4 was the peak of the shifted downstream profile.) There was no statistically significant difference between the two profiles in normalized capture for row 5. Other comparisons (symmetrical *vs.* shifted upstream, symmetrical *vs.* shifted downstream, shifted upstream *vs.* shifted downstream) showed a common pattern—the rows located upstream of *both* peaks were indistinguishable in terms of normalized particle capture. Furthermore, rows located downstream of both peaks (rows 4 and 5 for symmetrical *vs.* shifted upstream; row 5 for the other two combinations) consistently showed no significant differences in normalized particle capture.

Cross-profile comparisons can be summarized as follows: (1) There were always significant differences in capture by peak and upstream rows between the flat *vs.* hill-shaped profiles. (2) In contrast, there were no significant differences in particle capture by those rows located upstream of the peaks of hill-shaped profiles. (3) *All* cross-profile comparisons confirm that there is no statistically significant difference in capture by rows downstream of the peak(s).

To compare absolute capture rates of the mock barnacle arrays, either the symmetrical or shifted downstream array and the flat array were placed in the flow tank simultaneously. Placing two arrays in the flow tank at the same time caused the arrays to be nearer the walls and hence a change in flow patterns would be expected; however, because the flow velocities in the tank are symmetric about the midline of the tank, these altered flow patterns are symmetric across the profiles and therefore do not invalidate comparison. The mean total row and array capture values are given in Table IV; the results of row-by-row and total capture paired Student's t-tests are given in Table V. These results mimic those described above. Most importantly, the rows located downstream of the peak showed no statistically significant difference in capture between the profiles. Both the symmetrical and the shifted downstream profiles captured about twice as many particles as the flat profile (Table IV); in both cases, the differences were statistically significant (Table V).

Clusters of living barnacles

Areas of the cirral baskets of the peak and downstream animals in Cluster I were comparable (within 20% of each other), as were the areas of the cirral baskets of the peak, upstream 1, and upstream 2 animals in Cluster II. The

Table IV

Mean particle capture of simultaneously tested mock barnacle arrays

	Symmetrical	Flat	Shifted downstream	Flat
Row 1	(29.3 ± 7.4)	(49.7 ± 17.5)	(21.9 ± 5.2)	(39.6 ± 8.7)
Row 2	32.3 ± 10.5	3.2 ± 1.5	33.4 ± 8.4	2.1 ± 0.7
Row 3	74.8 ± 22.2	4.0 ± 1.1	9.3 ± 2.4	1.6 ± 0.5
Row 4	(2.5 ± 0.8)	(4.7 ± 2.3)	32.4 ± 10.4	1.4 ± 0.6
Row 5	(2.8 ± 0.7)	(3.3 ± 1.7)	(0.4 ± 0.3)	(1.7 ± 0.7)
Total	142.2 ± 40.9	64.8 ± 23.0	97.4 ± 24.2	46.4 ± 9.7

The symmetrical array was tested against the flat array in six trials; the shifted downstream array was tested against the flat array in seven trials. Mean values of particles caught are given by row and for the total array. Paired values for the two arrays which are not significantly different from each other (see Table V) are given in parentheses.

Table V

Paired Student's t-tests of differences in particle capture for mock barnacle arrays tested simultaneously in the flow tank

	Symmetrical *vs.* Flat		Shifted down *vs.* Flat	
	t-value	*P*	t-value	*P*
Row 1	−1.920	0.113	−2.107	0.080
Row 2	3.206	0.024	3.887	0.008
Row 3	3.312	0.021	3.471	0.013
Row 4	−1.245	0.268	3.064	0.022
Row 5	−0.324	0.759	−1.486	0.188
Total	4.065	0.010	2.829	0.030

For the symmetrical *vs.* flat arrays, n = 6; for the shifted down *vs.* flat arrays, n = 7. In all cases, a two-tailed test was used.

cirral basket of the downstream animal of Cluster II was approximately half the size of those of the upstream 1, upstream 2, and peak animals. The peak and upstream animals of Cluster III were comparable in cirral basket area, but the cirral basket of the downstream animal was approximately two-thirds the size of those of the peak and upstream animals. For all three clusters, animals in the upstream and peak locations were clearly passively suspension feeding, while all animals downstream of the peak were clearly actively beating their cirral baskets.

For Cluster I, unpaired Student's t-tests (Table VI) indicated that both capture rates and cirral beat frequencies of the peak and downstream animals were significantly different ($t = 5.06$, $P = 0.002$ and $t = 54.159$, $P < 0.001$, respectively). For Cluster II (Table VI), ANOVA of relative capture rates was highly significant ($F_{3,12} = 15.377$, $P < 0.001$); using Fisher's protected least significant difference (PLSD) test, upstream 1, upstream 2, and peak animals were not significantly different in capture rates, but all three animals were significantly different from the downstream animal. ANOVA of cirral beat frequencies for Cluster II was also highly significant ($F_{3,25} = 44.065$, $P < 0.001$). Using Fisher's PLSD test, two animals (upstream 1 and upstream 2) were not significantly different in cirral beat frequencies; all other combinations of animals were significantly different from each other. ANOVA of relative capture rates for the animals in Cluster III (Table VI) was also highly significant ($F_{2,9} = 16.566$, $P = 0.001$). Using Fisher's PLSD test, the upstream, peak, and downstream animals were all significantly different from each other in capture rates. ANOVA of cirral beat frequencies was highly significant ($F_{2,18} = 298.69$, $P < 0.001$). Using Fisher's PLSD test, the upstream and peak animals were not significantly different from each other in cirral beat frequency, but both animals were significantly different from the downstream animal.

Figure 2 (A–C) presents the flow patterns and associated local velocities around the three live barnacle clusters. The qualitative flow environment of peak and upstream animals differed from that of downstream animals. Whereas the path lines upstream and over the peak of the clusters in Figure 2A–C were smooth, continuous, and long, those downstream were convoluted, discontinuous, and punctuated in length; a highly disordered, turbulent flow region (the wake) was present immediately downstream of all clusters. Local flow velocities also differed. The flow velocities in the upstream and peak areas of the clusters was approximately 2.0–5.5 cm/s; flow velocity in the turbulent region downstream of the clusters was approximately 0.3–1.5 cm/s.

Discussion

Hydrodynamic simulation

The flume used in this study was too narrow to accurately reproduce the essentially two dimensional flow typical of the ocean bottom; for such purposes, the width to depth ratio of the flow should be greater than 5:1 (Nowell and Jumars, 1987). However, because our interest was in the flow around a cluster rather than cluster-sediment interactions, and because the velocity profile was essentially flat across the center two thirds of the flume in both depth

Table VI

Artemia *nauplii capture rates and cirral basket beat frequencies for selected* Balanus amphitrite *individuals in three clusters*

	Mean capture/ 3 min	n	Feeding mode	Mean beats/s	n
Cluster I					
upstream	—	—	—	—	—
peak	6.75 ± 0.75	4	P	0.5 ± 0.03	6
downstream	2.75 ± 0.25	4	A	2.9 ± 0.03	7
Cluster II					
upstream 1	5.75 ± 0.85	4	P	1.3 ± 0.14	8
upstream 2	7.00 ± 1.29	4	P	1.7 ± 0.12	8
peak	6.50 ± 0.29	4	P	1.4 ± 0.11	6
downstream	0.25 ± 0.25	4	A	2.9 ± 0.02	7
Cluster III					
upstream	17.00 ± 2.27	4	P	1.3 ± 0.04	10
peak	9.00 ± 1.47	4	P	1.1 ± 0.08	6
downstream	3.75 ± 0.85	4	A	2.9 ± 0.02	5

Values given are means ± the standard errors of the means. Upstream and downstream animals were located on the leading and trailing edges of the clusters, respectively; peak animals were located on the highest points of the clusters (see Fig. 2). Feeding modes [active (A) or passive (P)] of each animal are indicated. Cirral basket areas of the peak and downstream animals in Cluster I were within 20% of each other, as were the cirral basket areas of the peak and upstream animals in Cluster II and Cluster III. The cirral basket of the downstream animal of Cluster II was approximately half the size of the other animals in the cluster; the cirral basket of the downstream animal in Cluster III was approximately two-thirds the size of the other animals.

and width, we believe that our laboratory experiments are representative of the field situation. Both a single mock barnacle array and a live barnacle cluster occupied about 25% of the width of the flow tank and 12–20% of the depth, but only about 4% of the total cross sectional area of the flow. Nowell and Jumars (1984, 1987) suggest that blockage effects will not be significant if the height of an obstacle to the flow is less than 35% of the depth of the flow and 25% of the width. For a flume of their recommended proportions, such an obstacle, semicircular in cross section, would block 4% of the area of the flume, the same value as both our models and live barnacle clusters.

When two mock barnacle arrays were placed simultaneously in the flow tank, they occupied at least 50% of the width of the tank and 8% of the cross section. Significant alteration of the flow patterns certainly occurred, and portions of each array were overlapped by the boundary layers on the side walls of the flume. Because both arrays were equally affected, these flow modifications do not compromise the comparisons we make between the arrays. The fact that the row-by-row relative capture patterns of profiles tested singly in the tank are in accordance with the results of two arrays tested simultaneously implies that the patterns of particle capture in these arrays are relatively immune to details of the flow regime, although absolute capture values will certainly be affected.

Barnacles apparently acclimate to the ambient flow regime; when exposed to altered flow velocities or flow cycles, they may refuse to feed until they become acclimated to the new conditions (Trager *et al.*, 1990). This would help explain the existence of a range of mainstream flow velocities below or above which the barnacles in our study were reluctant to feed. At mainstream velocities greater than around 7 cm/s, the barnacles in our study retracted into their test, while at mainstream velocities less than 1 cm/s, the barnacles would often beat and retract in a nonrhythmic fashion. We take this as indirect evidence that the clusters in our study had been exposed in the field to a mean mainstream flow velocity of 4–5 cm/s and believe that the single value we have for field flow velocity reflects typical conditions.

Mock barnacle arrays

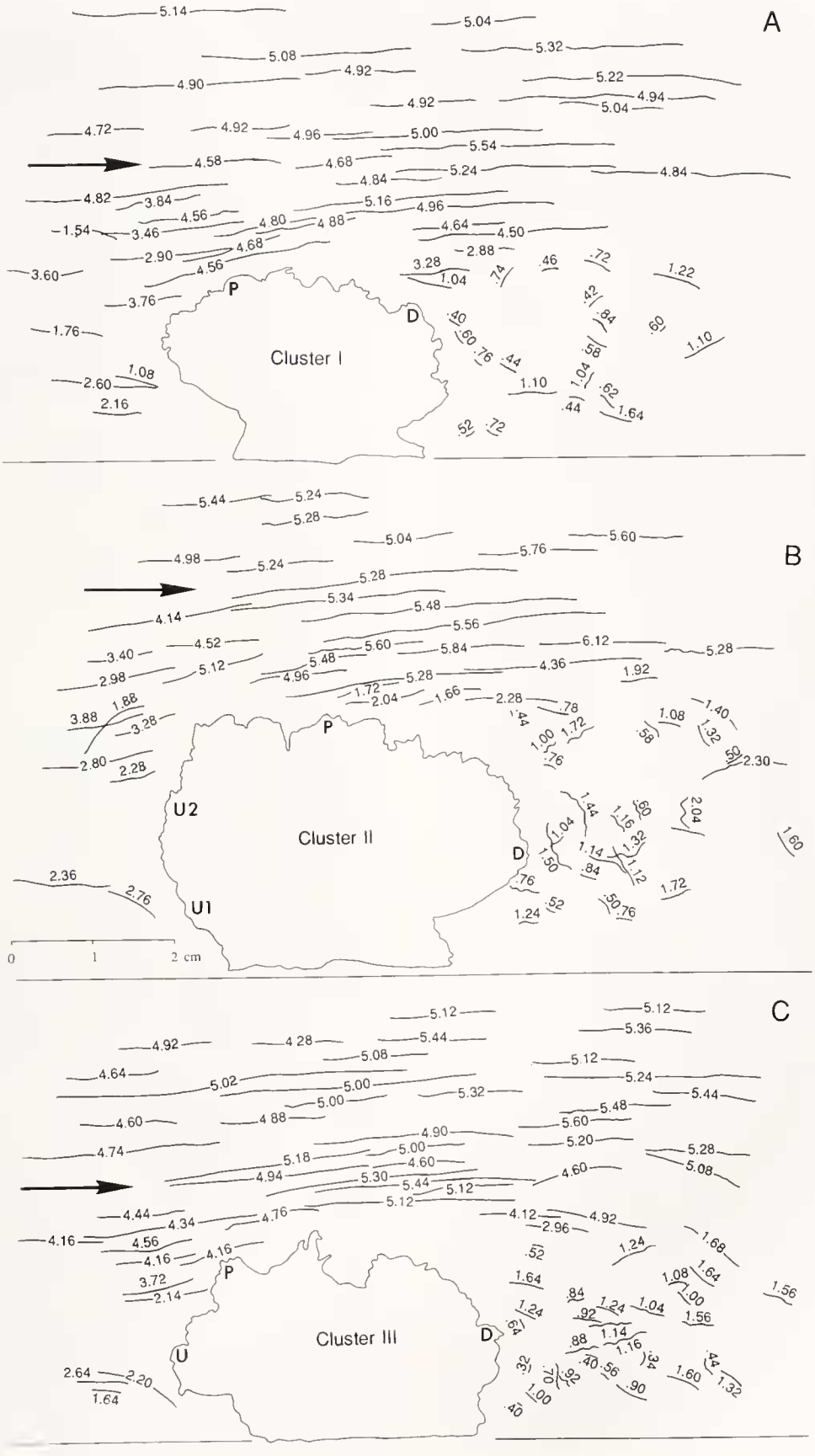
In terms of particle capture, the mock barnacle arrays exhibited the following general features: (1) For hill-shaped profiles, the peak row and each row upstream of peak generally captured a significantly higher proportion of the total particles captured than did rows downstream of the peak, regardless of the particular profile of the array. For the flat profile, the extreme upstream row was functionally a "peak," capturing a significantly higher fraction of the particles available than did rows downstream. (2) Rows downstream of peaks showed no significant differences in proportional particle capture among themselves, regardless of the specific profile of the array. (3) Hill-shaped profiles captured significantly more particles as an entity than did flat profiles.

The triangular mesh used as a "cirral basket" mimic on the mock barnacles was an imperfect model of a barnacle cirral basket: (1) It was flat rather than concave upstream and thus is likely to be less efficient as a filter (Warner, 1977; Baumiller, 1988), and (2) the triangular shape we used was only a rough approximation of the outline of a barnacle's cirral basket (the distal edge of cirral baskets is an arc rather than a straight line). The mock barnacle arrays only mimicked barnacles passively suspension feeding; it was not possible to represent actively feeding barnacles. Because barnacles show plasticity in feeding behavior, the feeding behavior and feeding ability of live barnacles in a cluster must be considered before conclusions can be drawn from these modeling studies about the location-dependent feeding of barnacles.

Positional effects on feeding in living barnacles

It is clear that live barnacles in a cluster displayed differential feeding behavior that was correlated with location in the cluster. Those barnacles surveyed at upstream and peak locations displayed a significantly lower cirral basket beat frequency than did those barnacles situated downstream. No differences between upstream and peak locations in cirral beat frequency could be demonstrated. The mechanistic link between barnacle location and behavior is local flow environment; barnacles tend to be active feeders in slow flow environments (<2–3 cm/s) and passive feeders in higher velocity flows (>2–3 cm/s) (Crisp and Southward, 1961; Trager *et al.*, 1990). Figure 2A–C documents the linkage between barnacle location in clusters and local flow environment. The downstream turbulence apparent in the figure apparently arose from vortices shed from the cluster, a feature common to bluff bodies in flows at moderate to high Reynolds numbers

Figure 2. Streamlines and local flow velocities around the three *Balanus amphitrite* clusters observed. (A) Cluster I. (B) Cluster II. (C) Cluster III. All clusters were observed in a unidirectional, laminar flow of approximately 5 cm/s mainstream velocity. Note that flow is laminar and similar in speed to mainstream flow for regions of the clusters upstream or at the peak in height of each cluster, but that flow is turbulent and markedly reduced in speed in the wake of each cluster, downstream of the peaks. The locations of the barnacles whose feeding and beat frequency were quantified (Table VI) are indicated (U = upstream, P = peak, D = downstream). Direction of mainstream flow is indicated by arrows.


A
Cluster I
P
D
B
Cluster II
P
U2
U1
D
0
1
2 cm
C
Cluster III
P
U
D

(Vogel, 1983). The Reynolds number for a cluster of barnacles 2–3 cm in length exposed to a flow of 5 cm/s is on the order of 10^3. Although this study was carried out only at a mainstream flow velocity of 5 cm/s, the flow dynamics will obtain for velocities much higher than this. Absolute velocities at different sites on a cluster will, of course, be a function of mainstream velocity, but the qualitative differences in flow pattern upstream and downstream of the peak of a cluster and the strongly reduced velocities downstream of the peak should be present in a broad range of mainstream velocities.

The observed flow dynamics around clusters provides an explanation for the location-dependent food capture and feeding behavior differentials. Whereas barnacles located upstream and at the peak of a cluster will experience a high flux of particles due to the high flow velocity through their cirral baskets, barnacles located downstream in a cluster will see a lower flux of particles because of both the decrease in local flow velocity and the recirculation of fluid in the cluster's wake. Our data indicate that living barnacles in an upstream or peak position capture significantly more particles than those in a downstream position. No differences between upstream and peak locations in particle capture could be demonstrated. Barnacles located at upstream and peak locations need only hold their cirral nets against the flow to feed successfully. In contrast, barnacles located downstream must create their own feeding currents by actively beating their cirral baskets. The faster beat frequency and the qualitative difference in cirral motion implies a higher rate of metabolic activity on the part of downstream animals during feeding, but even given this increased activity, they exhibit significantly reduced feeding success.

Patterson (1984) studied the location-dependent feeding success of a passive suspension feeding colonial octocoral, *Alcyonium siderium*. His work demonstrated greater capture success by upstream polyps when the mainstream flow was slow (2.5 cm/s), equal capture by upstream and downstream polyps at an intermediate flow velocity (9.0 cm/s), and greater capture by downstream polyps when the flow was rapid (19 cm/s). The morphology of *Alcyonium* colonies modified the flow as it passed through the colony; flow was decelerated as it encountered the closely spaced polyps and feeding tentacles (Patterson, 1984). The flow experienced by most of the colony was both more complicated and substantially reduced in speed from the mainstream flow. Patterson (1984) suggested that these alterations in the pattern of feeding success as flow velocity increased might be due to changes in the contribution of turbulence to the eddy diffusion of food particles in the vicinity of downstream polyps. By contrast, many of the barnacles in a cluster experience quasi-mainstream flow, and our observations, although only conducted at a single flow speed, indicate that turbulence downstream of barnacle clusters does *not* increase food supply to downstream barnacles. We believe that the contrast between our results and Patterson's arises, in part, from the difference in mechanical compliance of octocoral polyps and individual barnacles. The plasticity of the octocoral colony due to polyp deflection in response to flow-induced forces may interact with the downstream turbulence to create particle transport conditions that are not present in the case of barnacle aggregations. Deflection in response to current-induced drag forces also seems to underlay differences between food capture rates of the hydroid *Obelia* in unidirectional and oscillating flows (Hunter, 1989). In unidirectional flow, hydroid colonies were bent over and pressed toward the substrate; in oscillating flow, the colonies remained relatively upright, bending from side to side (Hunter, 1989). Deformation resulting from flow-induced forces can have a profound influence on both local flow patterns (Harvell and LaBarbera, 1985) and feeding rates (Sponaugle and LaBarbera, 1991) of passive suspension feeders. However, because of their rigidity, on short (seconds) to medium (days to weeks) time scales where differential growth of individual barnacles can be ignored, the flow patterns around barnacle clusters are fixed.

The ontogeny of barnacle cluster shapes

Barnacles are sessile animals. Though barnacle cyprids typically have a prolonged competent period to sample settling sites, once a barnacle cyprid cements to the substrate, it is committed to remain with the aggregation it has joined or that develops around it (Buss, 1981). Because the extreme upstream row in a flat mock barnacle array captures significantly more "food" than downstream rows, upstream animals in an even-height cluster of living barnacles should grow taller than downstream animals. The peak and rows upstream of peak of hill-shaped clusters of either mock or living barnacles feed considerably better than rows downstream of peak; living barnacles in regions upstream of, or at the peak of, a cluster should show higher growth rates than animals in downstream regions, thus exaggerating height differences over time. This implies that, in a unidirectional flow, the shifted upstream profile is the stable configuration; *i.e.*, in unidirectional flow, all profiles should tend, over time, to grow into the shifted upstream profile. In nature, strictly unidirectional flow past barnacle aggregations is probably rare, but barnacles experience strictly unidirectional flow on ship hulls and in pipes through which water is pumped by human activities (*e.g.*, the seawater systems in marine laboratories, the cooling systems of power generating plants). We predict that shifted upstream profiles would be the dominant shape of groups of encrusting barnacles in these flow situations, but data are lacking to check this prediction.

All of our data was obtained in a unidirectional flow regime, but barnacles in nature experience various combinations of unidirectional and bidirectional flows. Caution must be used in extending data obtained in one flow regime to a different flow regime. At least two aspects of oscillating flows are potentially significant for suspension feeding animals—the alteration in flow direction *per se*, and the effects on flow patterns (Denny, 1988) of the forces that arise when fluids are accelerated. The influence of acceleration effects in oscillating flow on the flow patterns can be assessed via the period parameter, K (Denny, 1988), where $K = u_m T/L$ (u_m is the maximum velocity in each direction of flow, T is the period of oscillation and L is the characteristic length of the cluster). In a wave-swept subtidal or intertidal environment, the period parameter, K, for a barnacle cluster may be large. [For example, a cluster of *Balanus amphitrite* 3 cm in diameter in a (mainstream) flow of 5 cm/s oscillating with a period of 15 s would yield a K of 25.] This means that, in one oscillation, the flow travels a distance longer than the length of the cluster; that is, the flow can be considered to be essentially steady (Denny, 1988). The influence of waves of shorter periods, which tend to dominate in intertidal protected areas, could not be approximated by steady flow, but the flows in such protected environments are more likely to be dominated by tidal than wave-generated currents. Thus the flow patterns around a cluster in oscillating flow will probably not differ substantially from the flow patterns resulting from the unidirectional, steady flow we used in our investigations. At the level of the individual barnacle, the length scale is smaller and K is thus larger. In addition, the cirral basket of barnacles has distinct polarity (concave upstream) and is actively oriented into the flow. Barnacles must reorient the cirral basket when flow direction reverses; by the time a barnacle does so, the flow will be essentially steady and the effects of accelerated flows will be unimportant. Hence justification exists for extrapolating our data to predict the shape of barnacle cluster profiles in oscillating flow.

Even though the effects of fluid acceleration on flow patterns around individual barnacles and barnacle clusters are probably not large in most situations, the effects of change in flow direction *per se* will still be patent. Because upstream and downstream rows will be reversed every half period of oscillation, an end row of the cluster will only receive the benefits of being an upstream row half the time; the average food capture of an end row will be diminished relative to the peak row. In a unidirectional flow, the extreme upstream row of the symmetrical profile captures approximately 60% as many particles as the peak row (Table I). In oscillating flow, this value would be averaged with the value for the extreme downstream row; the end rows of a symmetrical profile would, on average, capture approximately 35% of the particles caught by the peak row. In oscillating flows, a shifted upstream profile is functionally transformed into a shifted downstream profile on flow reversal and *vice versa;* the two profiles actually represent alternative views of the same asymmetrical profile in an oscillating flow. From the data on our model arrays, the extreme row closest to the peak in such an asymmetrical profile should average 53% of the average particle capture of the peak row, while the extreme row furthest from the peak should average 43% of the average capture of the peak row. Similar logic can be applied to the live barnacle clusters. For example, if in Cluster II the two upstream animals switched positions with the downstream animal on flow reversal, these animals would capture, on average (correcting for differences in area of the cirral baskets), about 53% of the particles caught by the peak animal (Table VI). In Cluster III, if the upstream and downstream animals exchanged positions on flow reversal, these animals would, on average (again correcting for size differences), capture approximately the same number of particles as the peak animal; however, note that the peak animal would capture these particles exclusively by passive suspension feeding, while the other animals would spend half of their time actively beating with a concomitant increased cost. In an oscillating flow (whether of short period—from waves, or long period—from tides), all profiles should tend over time to grow into the symmetrical profile. Barnes and Powell (1950) encountered symmetrical barnacle hummocks near the shore in areas exposed to both tides and wave action. Their observations are consistent with our prediction that symmetrical hummocks should form from prolonged exposure of aggregations of barnacles to oscillating flow.

The data from both mock barnacle arrays and clusters of living *B. amphitrite* indicate that aggregations of barnacles will grow into hill-shaped clusters due to the interactions of cluster shape, flow, and feeding. Location in a cluster determines the local flow environment of a barnacle which, in turn, is the proximate cue determining the barnacle's feeding behavior (active or passive). Note the positive feedback present in this situation. Barnacles feed passively by virtue of the fact that their local flow environment is relatively rapid (*i.e.*, above threshold for passive feeding), and the local flow environment is relatively rapid because the barnacle is located at the peak or upstream end of the cluster. Passive suspension feeding is correlated with more successful feeding; successful feeders grow more rapidly and thus draw the cluster further towards one of the hill shaped profiles. Active suspension feeding is a metabolically more expensive (and apparently less successful) mode to which barnacles apparently resort only when ambient flows are too slow to deliver food particles at some minimal rate. The precise shape of a barnacle cluster will depend on the flow situation. A cluster with its peak shifted upstream will be the

stable shape for an aggregation of barnacles in a unidirectional flow, while a symmetrical cluster will be the stable end point of the evolution of cluster shape for barnacles in an oscillating flow.

Barnes and Powell (1950) noted that barnacles in the center of hummocks become elongated to the point that they are often dislodged. Because barnacle cyprids preferentially settle in areas already populated by barnacles or barnacle remains (Knight-Jones, 1953; Wethey, 1984), the areas previously occupied by the dislodged barnacles would recruit a new settlement of barnacles and the growth of the aggregation form would be subject once again to the influence of feeding and flow.

Hill-shaped arrays do better at feeding as a unit than flat arrays. This indicates that there may be benefits to a barnacle in being in a hill-shaped aggregation even if that barnacle is not located at the peak. This will be true particularly for clusters in oscillating flow, for there will be a perpetual alternation of the barnacles favored by rapid flow, leading to a more balanced distribution of good feeding fortune across the whole cluster than in unidirectional flow.

A barnacle's position relative to flow is crucial in determining its relative and absolute feeding success in an aggregation. It is location-dependent differential food capture between individual barnacles in an aggregation that gives rise to the morphology of the whole aggregation. Although our data on living barnacles are limited to a single species, we believe that the patterns of flow and of feeding success we describe will be true for any aggregation of acorn barnacles in which some of the individuals in the aggregation are exposed to local flow speeds high enough to elicit passive suspension feeding. We suggest that the shape of barnacle aggregations will generally tend, via growth and recruitment of individuals, toward stable forms that are determined by the flow regime—shifted upstream for unidirectional flow, or symmetrical for oscillatory flow.

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